Ayres: Effects of Fire on Three Rare Plants
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EFFECTS OF FIRE ON THE DEMOGRAPHY OF THREE RARE CHAPARRAL PLANTS (*CALYSTEGIA STEBBINSII*, *CEANOTHUS RODERICKII*, AND *WYETHIA RETICULATA*)

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ABSTRACT

Wyethia reticulata (Asteraceae), *Ceanothus roderickii* (Rhamnaceae), and *Calystegia stebbinsii* (Convolvulaceae) are rare plants endemic to the gabbroic chaparral of western El Dorado County, California. All three are threatened by on-going residential development and fire suppression. I examined vegetative growth and flowering of these species before fire, and the survival, growth, and development of seeds, seedlings, and resprouted stems after fire. Fire was necessary for recruitment from seed in all three species. While seedling recruitment may not be required for maintenance of extensively clonal, resprouting *W. reticulata* populations, without fire-stimulated germination, populations of both *C. roderickii* and *C. stebbinsii* were mostly represented only in the seed bank in mature chaparral. Recovery patterns of other species of obligately seeding chaparral species suggest that in addition to habitat loss, a principle threat to species in this functional group are short-interval fires. Short-interval fires kill young plants before seed banks have been replenished with the result that these species are eliminated from the site. Fuel for short-interval fires is provided by exotic annual grasses that invade or are sown into burned sites. Conservation strategies for these species will involve management of the chaparral system in accord with varied functional responses of plants to fire, and suppression of annual grass invaders to avoid short-interval fires. It will be necessary to create several preserves to mitigate against disease and insect epidemics, and to guard against short-interval fires wiping out the entire species.

Key words: chaparral, fire management, obligate resprouter, obligate seeder, rare plants.

INTRODUCTION

Chaparral is a widespread, shrub-dominated community in California (Keeley and Keeley 1988). Under a Mediterranean climate, moderate wet winters favor shrub growth, while protracted summer drought makes the community susceptible to ignition by lightning or humans. Shrubs and herbaceous perennial plants native to this community have been traditionally categorized according functional type, that is, the means whereby they survive fire. Subterranean structures (bulbs, rhizomes, tubers) allow some species to resprout after fire ("obligate resprouters"), while other species have seeds capable of withstanding high soil temperatures that germinate after fire. Species with adult mortality caused by fire exhibit an "obligately seeding" life history strategy as they rely solely on a seed bank for regeneration. Many species regenerate from both seeds in the soil and underground perennating structures; these species have been termed "facultative seeders". Recently, an approach which considers plant life form within the context of these functional types has been advocated as a way to understand more completely the dynamics of postfire succession in chaparral (Keeley et al. 2006). For example, the response of obligately seeding woody shrubs is quite different from obligately seeding annual forbs due to differences in the time required to reach sexual maturity, e.g., several years in woody shrubs versus a single season for annual forbs.

The chaparral on a "geological island" of gabbro soil in El Dorado County, which encompasses around 104 km^2, has been recognized as a distinct community type in California—gabbroic northern mixed chaparral (Holland 1986). The gabbro soil was derived from a volcanic intrusion of gabbroic rock during the Mesozoic (approx. 175 million years in age) and the geological island is surrounded by soils of mostly metamorphic origin (Springer 1968). Northern gabbroic chaparral is dominated by the shrubs *Adenostoma fasciculatum* Hook. & Arn. and *Arctostaphylos viscida* Parry, and is home to the plants considered in the present study: *Wyethia reticulata* Greene, a species of concern, and *Calystegia stebbinsii* Brummitt and *Ceanothus roderickii* W.Knight, species on the federal endangered species list. Two other federally listed species occur in the gabbro chaparral, endangered *Fremontodendron californicum* (Torr.) Coville subsp. *decumbens* (R.M.Lloyd) Munz and threatened *Senecio layneae* Greene. Among the principal threats

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to the rare species are continuing loss of habitat due to urbanization, road building, invasion by exotic weeds, and the suppression of periodic natural fires (United States Fish and Wildlife Service [USFWS] 1996).

The presence of several listed species, sharing the same habitat and facing similar threats, has led to the community-level preservation strategy adopted by the USFWS that is the major prescription in the recovery plan for these gabbro species (USFWS 2002). The recovery plan is based on patterns of species distribution, habitat quality, and general approaches to preserve design, and incorporates current knowledge of the biology of individual species. The present study provides further demographic detail on species covered by the recovery plan.

The purpose of this study was to investigate the response of three rare chaparral plant species to fire. I measured survival, vegetative growth and flowering of established plants, tested the survival of buried and unburied seed following experimental fires, and monitored seedling recruitment, survival, and growth following experimental and accidental fires in mature chaparral.

MATERIALS AND METHODS

Study Species

Wyethia reticulata (hereafter *Wyethia*) is a long-lived herbaceous perennial that spreads by underground rhizomes. Previous work using molecular fingerprints showed that populations consist of a relatively small number of genetic individuals, each of which covers 10s to 100s of m^2 (Ayres and Ryan 1997). The species' range is entirely within the gabbroic-chaparral community in El Dorado County, CA. Under a mature chaparral canopy, *Wyethia* is of short stature and rarely flowers. After fire or grading, the plant responds by vigorously resprouting and flowering.

Ceanothus roderickii (hereafter *Ceanothus*) is a prostrate, evergreen shrub also restricted to the gabbroic chaparral in El Dorado County. In open sites, plants flower profusely and can spread up to 3 m (Hickman 1993, and pers. obs.). Plants are infrequent and flower sparsely under the mature shrub canopy (pers. obs.), are killed by fire, and recruit from seed the spring following fire (Boyd 2007), fitting the life history pattern of an obligate seeder.

Calystegia stebbinsii (hereafter *Calystegia*) is an herbaceous perennial with trailing and climbing stems arising from underground rhizomes and slightly woody caudices (Hickman 1993). It grows primarily within the gabbroic-chaparral community in El Dorado County, but has an additional small population to the north in Yuba County. Plants can be found along firebreaks and roadsides, but are absent from the adjacent intact mature chaparral (pers. obs.). Seedling recruitment occurs after fire from seeds in the soil.

Description of Sites

The Rescue site (near the town of Rescue, California) was near the center of the gabbro chaparral and was burned during a wildfire in August 1990. There were no records of when the site burned previously, but a count of 82 rings was made from the trunk of a *Quercus kelloggii* Newb. killed by the 1990 fire. This site was monitored for both *Wyethia* and *Ceanothus*; *Calystegia* does not occur in the central portion of the gabbroic chaparral.

Plots were established at four sites in the northern range of the gabbro-chaparral community south of Pilot Hill, near Salmon Falls Road. Salmon Falls A and B (SFA and SFB) plots were established in May 1993 on sites ca. 500 m apart that had been burned during controlled fires in November 1991, and were monitored for *Wyethia* and vegetation only as the two other species did not occur there. Fire records indicate that the site had last burned in 1935. Salmon Falls C and D sites were burned as part of this study.

Experimental Fires

Plots were established at Salmon Falls C and D (SFC, SFD) in 1994, prior to their burning during experimental fires in October 1994. Fire records indicate the area had last burned in 1937. Unburned sites adjacent to the two experimentally burned populations were also sampled. SFC and SFD were separated by less than 100 m. Sites were chosen based on the presence of *Wyethia* and *Ceanothus* prior to burning; there were no plants of *Calystegia* present before the fire. The SFC plots were burned by the California Department of Forestry and Fire Protection (CDFFP) on 24 Oct 1994; on 31 Oct 1994, the CDFFP burned the SFD plots.

During the fires the maximum temperature at the surface and 2–3 cm below the surface of the soil was measured using Temperature-Indicating crayons (Omega Engineering, Stamford, CT) that melt when a specific temperature is reached. Twenty-eight crayons, spanning a range of temperatures from 52°C to 982°C, were cut into chips. The chips were glued

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(Crazy Glue) to galvanized steel plates measuring 13 × 18 × 0.015 cm. Each specific temperature chip occupied a fixed position on the metal plate. I placed 12 plates on the soil surface under the shrub canopy; four of these positions also had a plate buried 2–3 cm under the soil at SFC. SFD had 17 plates placed on the surface; six of these positions had subsurface plates as well.

Seed packets of each species were placed at each position with above and below ground plates to investigate the heat tolerance of seeds under field fire conditions. Ten seeds were placed in a small envelope made of aluminum foil; foil envelopes were placed inside a larger envelope made of aluminum screening. The seed envelopes were placed next to the metal temperature plates on and below the soil surface.

The seed packets and temperature sensor plates were recovered after the fire. The seeds from each foil envelope were placed on wet filter paper in a petri plate to observe germination. Control sets of seed were also included in germination monitoring. Petri plates with seeds of *Wyethia* and *Ceanothus* were placed at 5°C for six and eight weeks, respectively, prior to observation, to satisfy suspected cold-stratification requirements for germination in these species. Petri plates were kept at room temperature in dim light and examined daily for germinated seeds over several weeks.

Demographic Monitoring

Populations were monitored on sites that had burned; two sites (Salmon Falls C and Salmon Falls D) were burned as a part of this study (Table 1). Population changes were assessed by establishing permanent plots, 0.25 by 1.0 m, at sites inclusive of a large stand of *Wyethia*. Plot locations were randomly determined along transects equally spaced through the site. For all species, plots were assessed for established plants, flowering intensity, seedling occurrence, and juvenile survival and growth of the three species for up to six years after fire. Salmon Falls sites SFA, SFC, and SFD, were revisited 12 (SFC and SFD) to 15 (SFA) years after fire in 2006. SFC and SFD plots were assessed before and after the experimental fires, while assessments of SFA, SFB, and Rescue plots began two years after they burned. The total number of stems, the number of flowering stems, and the number of inflorescences per stem of *Wyethia* were recorded for the experimentally-burned sites, and for additional sites which had burned in other fires, described above. Individual plants of *Ceanothus* and *Calystegia* plants were considered to be the aggregation of stems that arose from within a circle 3–4 cm across. In *Ceanothus*, individual prostrate stems rooted at the nodes after 3–4 years; these were counted as “new” plants. Similarly, underground stolons in *Calystegia* produced “new” plants after two years. Data on juvenile plant growth of *Ceanothus* 2–8 years after fire were obtained from the site near Rescue.

Each spring plots were inspected for germinated seedlings. Only plants with cotyledons were counted as seedlings. For *Wyethia* only, when a new seedling was found, a metal stake ca. 5 cm long, made from a plastic-coated wire coat hanger, was inserted into the soil next to the seedling. Each year a different color stake was used to distinguish each cohort. The survival of two cohorts of *Wyethia* seedlings that germinated the second year following fire was evaluated. These measures to distinguish cohorts were not needed for the other two species as there was virtually no germination after the first flush of seedlings in the spring following fire.

Vegetation Composition and Cover

Vegetation was surveyed at each fire site in the month of June every year from 1992 until 1996. A record was made of all vascular plant species, and cover values were assigned on a Braun-Blanquet scale (as described in Mueller-Dombois and Ellenberg 1974). Percent cover of the site by each vegetation layer (herb, shrub, and tree) was visually estimated. In 2006, vegetation was again surveyed at SFA, SFC, and SFD using similar methodology.

RESULTS

Maximum surface temperatures during the experimental fires ranged from 427°C to greater than 982°C; subsurface temperatures ranged from less than 52°C up to 242°C with a substantial fraction of the sensors (7/10) registering temperatures less than 100°C. All seeds on the surface were killed by the experimental fires, but many buried seeds survived. Each species had a characteristic germination response to temperature. For *Wyethia*, the control treatment seeds had the highest germination rate while subsurface temperatures of 93°C or above were lethal (Fig. 1). Over 80% of the seeds germinated where maximum temperatures were < 66°C; that percentage was halved when maximum temperatures reached 79°C. However, seeds survived at six of the ten positions where seeds were buried. *Calystegia*

Table 1. Site history, area sampled, number of sampled plots, and locations of populations considered in this study.

Site	Years burned	Size (m^2)	Number of plots	Location	
				Latitude	Longitude
Rescue (R)	1990 1908?	360	91	38°42'22"	120°59'22"
Salmon Falls A (SFA)	1991 1937	290	102	38°46'16"	121°00'25"
Salmon Falls B (SFB)	1991 1937	250	91	38°46'12"	121°00'25"
Salmon Falls C burned (SFC)	1994 1935	97	28	38°45'57"	121°00'25"
Salmon Falls D burned (SFD)	1994 1937	226	65	38°45'57"	121°00'25"

and *Ceanothus* seeds showed little or no germination without treatment. The optimum soil temperature for germination was 79°C for both species, and a small number of seeds germinated after exposure to temperatures in excess of 200°C (Fig. 1). Conditions favoring germination were found at seven of the ten subsurface positions. *Ceanothus* germination was greater at all temperatures than *Calystegia*. A small percentage (< 5%) of *Ceanothus* seed from the control treatment germinated following cold stratification only.

The intensity of flowering increased following fire in *Wyethia*, resulting in a > 20-fold increase in inflorescence density the first year after fire compared to pre-fire flowering at SFC and SFD (Fig. 2). While overall stem numbers remained elevated

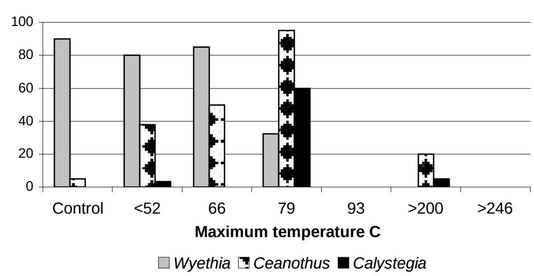

Fig. 1. Average percent germination of seeds of *Wyethia reticulata*, *Ceanothus roderickii* and *Calystegia stebbinsii* that underwent various temperatures during an experimental fire; control seeds did not experience the fire. Number of replicates varied from 2 to 6 per treatment

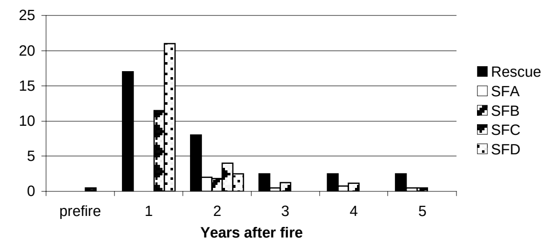

Fig. 2. Density of inflorescences of *Wyethia reticulata* from various populations before and following fire (SFA and SFB were not monitored in Year 1.

for years after fire, the proportion of those stems that flowered declined, resulting in a 70–85% reduction in density of inflorescences the second year following fire at SFC and SFD (Fig. 2), while flowering declined somewhat more slowly at the Rescue site. SFA and SFB, which were monitored from two to five years after fire, showed comparable reduction in inflorescence density to SFC and SFD. Data from all these sites, taken together, indicated that flowering remained low for at least six years post-fire. Seedlings of *Wyethia* were first seen on the burned sites during the second spring following fire; seedlings were not found immediately following fire or on undisturbed sites. Although the numbers of seedlings varied between sites, a general trend could be seen; peak number occurred two years after fire and declined thereafter (Fig. 3). Mortality of seedlings was high and young plants continued to die at a high rate (Fig. 4). Young plants were small and rarely had > 2 leaves, even after four years of growth.

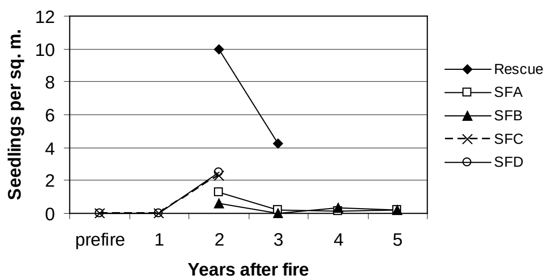

Fig. 3. Average density of seedlings per m^2 of *Wyethia reticulata* before and following fire

Fig. 4. Survivorship of five naturally occurring cohorts of seedlings of *Wyethia reticulata* after fire. Note y-axis is logarithmic and 1-year old plants are seedlings

Established *Ceanothus* plants, present at very low density prior to the fires, were killed by the fires at SFC and SFD. A moderate number of seedlings (3–7/m^2) were found the following spring (Fig. 5). At SFC all seedlings in the plots were dead by the second spring (1996); in 2006 there were ca. 0.02 plants/m^2 at the site with < 1% cover. At SFD, seedling numbers were reduced by more than half from the first spring (1995) to the second (1996), from about 7 plants in 1995 to ca. 3 plants/m^2 in 1996; in 2006, there were ca. 0.09 plants/m^2 with 7% cover. Most seedlings that survived the first two seasons were alive at the third. None were flowering. In 2006, plants were in fruit at both SFC and SFD. At Rescue, where the census began the second spring after fire, plant number generally increased from ca. 0.2 to 0.9 plants/m^2 and plant cover from 2 to 13% from 1992 to 1998 (Fig. 6); however, the increase was due to new plants arising from the rooted nodes of prostrate stems, not from new seedlings. The ability of this species to branch-layer (root at the nodes) is a unique recovery mechanism among the other obligately seeding species of *Ceanothus* (Boyd 2007). Only 6.5% of the stems were flowering eight years after fire.

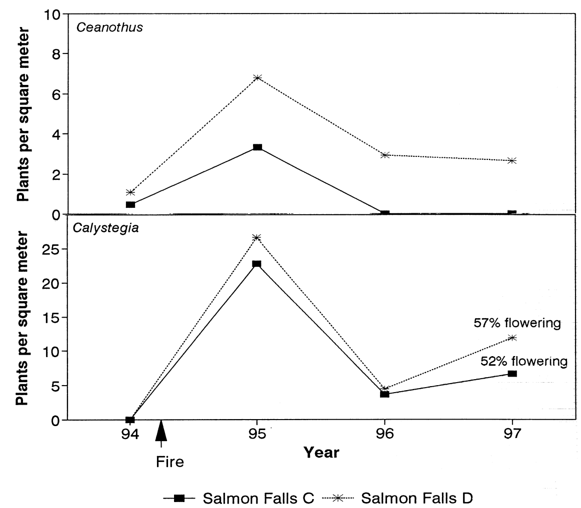

Fig. 5. Density of plants of *Ceanothus roderickii* (upper) and *Calystegia stebbinsii* (lower) before fire and density of seedlings following fire at Salmon Falls C and D.

Calystegia plants were not present before the experimental fires (Fig. 5). Large numbers of seedlings (25/m^2) were found in the spring of 1995 at SFC and SFD, six months after the experimental fires; 70–80% had died by the following spring. In 1997, three years after fire, the density of plants apparently increased, but the lack of cotyledons, plant size, and excavation of plants suggested that the increase was due to vegetative spread by stolons. Over 50% of the two-year-old plants flowered. In 2006, there were 0.009 plants/m^2 with < 1% cover at SFC, and 0.23 plants/m^2 with a cover of 2% at SFD.

Community cover assessments made before the experimental fires at the SFC and SFD study sites indicate almost total cover by shrub vegetation composed principally of *Adenostoma fasciculatum* and *Arctostaphylos viscida.* After a sharp post-fire decline, shrub cover increased gradually at all sites

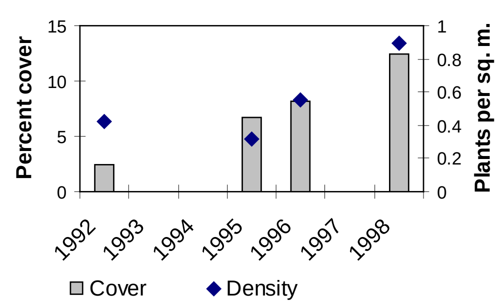

Fig. 6. Population growth (density of plants and average percent cover) of *Ceanothus roderickii* at the Rescue site (no data were taken in 1993, 1994 and 1997).

during successive years from resprouting species and from *Lepechinia calycina* (Benth.) Epling, which germinated after the fires (Fig. 7). Herb cover, low the year immediately following fire, increased substantially from the first to the second year after fire, and maintained at least 50% cover for the next 2–5 years (Fig. 7). *Wyethia* had the highest cover in the herb layer both before and after fire. By 2006, cover by shrubs 1–2 m tall had increased to 25% at SFC, while herb cover (< 40 cm in height) declined from 70% in 1994 to 25%. Shrub cover was dominated by *Ceanothus lemmonii* Parry (18% cover) and *Arctostaphylos viscida* (5%), while the herb layer was comprised mostly of *Wyethia* (15% cover) and *Salvia sonomensis* Greene (8%). The vegetation was quite different at SFD in 2006 where cover by shrubs, all < 1 m tall, was only 8% and was dominated by *Ceanothus roderickii* and short *A. fasciculatum*. Cover by herbs was 8% and consisted of *S. sonomensis* (5%), *Calystegia* (2%), and several species of annual, exotic grasses and forbs.

At SFA, 15 years after fire, herb cover had declined from a peak of nearly 80% in 1995 to 10% in 2006, while cover by shrubs 1–2 m tall increased only slightly from ca. 40% five years postfire to 43%. The shrub community at SFA was dominated in 2006 by *A. fasciculatum* (29% cover) with *Quercus durata* Jepson var. *durata*, *A. viscida*, and *Rhamnus ilicifolia* Kellogg each having ca. 5% cover. The herb layer was comprised mostly of *Salvia sonomensis* (4% cover) and *Wyethia* (5% cover).

DISCUSSION

Wyethia is an obligately resprouting herbaceous perennial. It survives fire because of an extensive underground rhizome system and the insulating properties of soil. Most rhizomes from which annual stems arise occur between 2 and 14 cm below the surface of the soil (Ayres 1997). This study and others (Sampson 1944; Boyd 1987) demonstrated the significant reduction in temperature that occurs within 1–4 cm of the soil surface. *Wyethia* responded to fire by a dramatic increase in flowering. Flowering declined to very low levels during subsequent years. This did not seem to be related to closure of the shrub canopy, but was coincident with high herbaceous cover, especially cover by *Wyethia*. The decline in flowering may have been due to the depletion of the nutrients released by the fire, and/or to intra- and interspecific competition for water during the late spring when *Wyethia* typically began to flower.

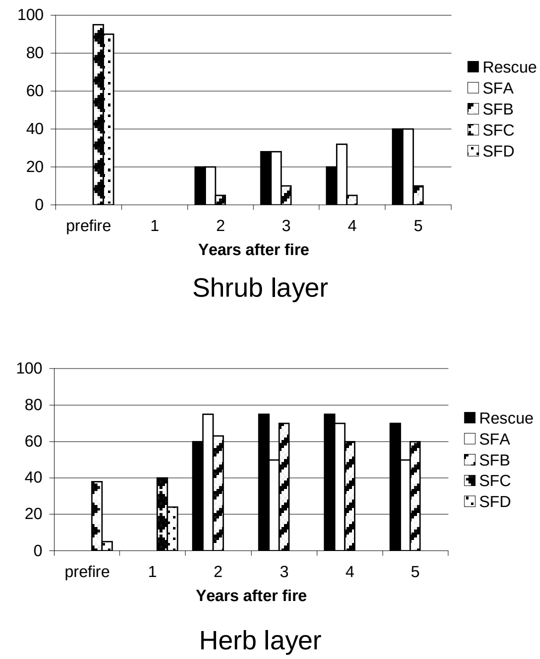

Fig. 7. Changes in vegetation cover of shrubs (upper) and herbs (lower) at various sites before and after fire.

The pulse of heavy flowering was followed, one year later, by peak numbers of seedlings. Seedlings were found primarily under the canopy of established *Wyethia* as the achenes have no obvious mechanism for dispersal. Seedlings were not observed in the spring following fire, despite their ability to survive fire when buried, indicating that *Wyethia* probably does not have a long-lived seed bank. Unlike seeds of other chaparral species which require high temperatures to germinate, the seeds of *Wyethia* were killed at temperatures of 93°C or above. The high germination rate of seeds exposed to moist chilling, comparable to what they would experience in the field over winter, suggested that the seeds do not possess a long-term dormancy mechanism. In addition, the achene has a thin fruit wall/seed coat, which may make it vulnerable to pathogens and predators and lessen its chances of surviving the interfire period. Therefore, sexual recruitment was from contemporary seed, produced by nearby plants, and primarily occurred during the second year after fire. Between fires, the populations are maintained by established rhizomes, not a seed bank.

Survivorship of naturally occurring seedlings on fire sites was low, and remained low throughout the duration of the study. Competition with herbaceous vegetation, including established *Wyethia*, may have been the cause of the high mortality, since naturally recruiting seedlings on fire sites first appeared during the second year after fire when herbaceous cover exceeded 60%. A consequence of historically low rates of seedling establishment will be stands of *Wyethia* composed of only a few genetic individuals as was found in genetic studies (Ayres and Ryan 1997).

Ceanothus roderickii is an obligately seeding woody shrub whose plants are killed by fire. Few plants were found under mature chaparral. I found seedlings only in the first spring following fire—a recruitment pattern identical to six other chaparral *Ceanothus* spp. (Keeley et al. 2006: Appendix A). Seed exposed to an experimental fire was capable of surviving temperatures in excess of 200°C, and seed from 7 of 10 buried sites survived. The appearance of abundant seedlings after wildfire in a ≥ 82-year-old stand of chaparral in Rescue suggests that seeds in the soil are capable of surviving for many decades. Although seedling mortality was high the first year, surviving plants grew well as the number of "plants" (rooted stems) and cover were increasing 4–8 years post-fire. This phenomenon was also seen by Boyd (2007) who suggested that postfire population recovery may be promoted by rooting of branches. In an earlier paper, Boyd (1987) found that almost all seedlings that appeared beneath an intact shrub canopy died (38/39), while those that germinated after fire both survived (136/841) and grew well. However, in the present study only 6.5% of the stems were producing flowers eight years after fire.

Studies on the population biology of *Ceanothus* species in southern California chaparral (Zedler et al. 1983; Zammitt and Zedler 1993) highlight the vulnerability to local extinction of obligately seeding species like *Ceanothus*. Maximum seed production in *C. greggii* was reached within two decades of fire, and was dependent on plant size, but *C. greggii* A.Gray is a canopy dominant, reaching heights of 2–3 m, whereas *C. roderickii* seldom grows higher than 0.5 m. Sunlight, especially morning sun, was required for the highest flower and fruit production in *Ceanothus* (James 1996). The interactions among seed production, plant size, and canopy closure may set an optimum fire return interval. On the other hand, fluctuations in seed production and predation may prevent the accumulation of seed in the soil of *C. greggii* (Keeley 1977) and in Northern California *Ceanothus* species (O'Neil and Parker 2005). Long-term studies (10–20 years postfire) tracking the dynamics of seed production, and seed input and longevity in the soil are needed in order to more precisely determine a fire return interval that will maintain *C. roderickii* populations in El Dorado County.

The response of several chaparral shrubs to a short-interval fire (one year apart) (Zedler et al. 1983) suggests that *C. roderickii*, like *C. oliganthus* Nutt. in San Diego County, could be eliminated from sites that burn too frequently. The second fire killed the seedlings that germinated in response to the first fire, and because the fire-cued germination response virtually eliminated the seed bank, no further recruitment occurred after the second fire. Given the low production of flowers 8 years postfire that I observed in this study, short-interval fires of ≥ 8 years might result in local extinction of *C. roderickii*. Other obligately-seeding members of the gabbro chaparral, such as dominants *Ceanothus lemmonii* and *Arctostaphylos viscida*, would also be eliminated by short-interval fires. *Adenostoma fasciculatum*, a species that both resprouts and has fire-promoted seed germination, did not fare much better than the obligately seeding species as its density was reduced by 97% following short-interval fires in San Diego County (Zedler et al 1983). Short-interval fires were fueled by dead, exotic, annual grasses. These grasses arrived on the burned site naturally, or by deliberate seeding to prevent erosion, and were ignited by arsonists or lightning. Recovery of the vegetation to chaparral after short-interval fires was predicted to take many years, and perhaps be impossible due to ongoing invasion by grasses that would promote re-burning of open sites.

Calystegia stebbinsii was absent before fire in my experimental plots, had seeds that survived temperatures in the soil in excess of 200°C, germinated profusely the first spring after fire, and began flowering heavily three years postfire. While this appears to be an obligately seeding functional type, a congeneric species, *Calystegia macrostegia* (E.Greene) Brummitt, from southern California chaparral is considered a facultative seeder (Keeley et al. 2006: Appendix A). Features in common for the two species include seeds that germinate primarily in the spring following fire, a twining and vining habit, and a woody caudex that, at least for *C. macrostegia*, was capable of surviving fire and resprouting. It remains to be seen whether *C. stebbinsii* can similarly resprout after fire. I found that the species was absent before fire, and that plant density declined over 98% from 1997 to 2006; these observations suggest that adult plants do not survive a long (> 10–20 year) inter-fire period.

Plant densities similar to those I found at three years postfire in the present study were found by Nosal (1997), who determined seed production at these densities to be 200–500 seeds/m^2. Considering that I found seed viability after fire to be around 60%, with a seedling density of 20–25 seedlings/m^2 in the field after fire, but without considering seed loss to predators, pathogens, fire, burial, or other causes of seed loss, *Calystegia* regeneration is calculated to require 33–42 seeds/m^2. Thus, since seed production was ca. 10-fold higher than this, it is possible that the seed bank for *Calystegia* is replenished after only a single year of flowering. Seed accumulation and survivorship studies would more precisely indicate the time required to replenish the seed bank. Given the possibility that *Calystegia* plants can resprout after fire, as suggested by its southern California congener, and the production of abundant seed within three years of fire, this species is likely not as vulnerable to short-interval fires as *Ceanothus*. It is unknown how long the seed can survive in the soil; however, my experimental plots were previously burned in 1937. Presumably, the seedlings in the present study arose from seed formed after that fire, suggesting seed longevity of six or more decades in the soil.

Genetic studies using isozymes found no evidence for genetic differentiation between populations of this species (Troutwine 1996), although DNA-based methods should be employed to further explore the question of genetic structure.

CONSERVATION IMPLICATIONS

Conservation of these species will require the establishment of several preserves to maintain the genetic structure of *Wyethia* (Ayres and Ryan 1997), and to mitigate against catastrophic losses due to fire, epidemics, etc. Preserves should be founded on sites that contain viable populations of the imperiled species because of the importance of long-lived individuals to the viability of *Wyethia* populations, and because of the reservoir of dormant seeds of *Calystegia* and *Ceanothus* present in the soil. Genetic data available for *Wyethia* (Ayres and Ryan 1997) suggested preserves should be created throughout the gabbro soil intrusion, including Pine Hill in the center, and sites in the north and south. Management of preserves will require periodic fires to stimulate the sexual reproduction of all three species, although this is probably not vital for *Wyethia*. The data presented in this study suggests that long fire intervals, in excess of 60 years, will not harm these species. Long-interval fires may be the most advantageous strategy in order to limit the years in which populations of *Ceanothus* and perhaps *Calystegia* are vulnerable to extinction by short-interval fires. Fueled by exotic, annual grasses, short-interval fires could result in the population extinction of all obligately seeding species. Therefore, annual grasses must be reduced, and the preserves protected from unforeseen fires during the early, vulnerable years following fire.

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